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Chapter

Morphological and Physiological Root Plasticity and Its Relationships with Shoot Growth of Rice with Water Regimes and Microbial Densities

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Abstract

There is renewed interest in root research for undergirding a second Green Revolution. The modular nature of root systems makes them amenable to both morphological and/or physiological plasticity when encountering heterogeneous environments. Such plasticity, the ability to change and adapt in response to variations in the underground environment, is linked to a shoot response and to consequent dry matter production, which is an important subject of research. This exploration is relevant in paddy production, especially in the context of climate change where rice production needs to be intensified with reduced water application and with reduced methane emission. This chapter reviews the plastic response of roots and illustrates some preliminary findings on the effects of biotic (soil microbes) and abiotic (water regimes) stimuli on root growth and activity and their relationships with shoot growth and its implications for mitigation of methane production without compromising grain yield.

Keywords: root plasticity, paddy, rice physiology, methane emission, climate change

1. Introduction

There is renewed interest in root research for undergirding a second Green Revolution. An article in *Nature* [1] reports on four of the most promising ways for boosting food production through modifications in roots: designer roots, stealth scavengers, microbial manipulation, and healthy fixation. All four ways, involving genetic manipulation of belowground traits, are undergoing evaluation. However, environmentally induced phenotypic variation in plants is often observed and is considered to be a functional response that maximizes fitness in variable environments. Such response is termed as reaction norms. The reaction norms may or may not be plastic. If it is plastic, then plasticity and reaction norms are used interchangeably. Basically, it refers to the set of phenotypes that can be produced by an individual genotype that is exposed to different environmental conditions [2].

Various studies have shown the modular nature of root systems that make them amenable to both morphological and/or physiological plasticity when encountering

heterogeneous environments. For example, a variety of crops proliferate roots in areas of high nutrient concentration, and that plant nutrient concentration and yield could be higher in heterogeneous soil than in homogenous soil [3, 4]. Increased uptake and growth responses were attributed both to root proliferation increasing uptake potential and to the fact that a given soil volume has the limited binding capacity and thus as nutrient supply increases [5]. Such root proliferation in response to locally elevated soil resource levels is simply one example of morphological plasticity to an environmental signal, one of many forms of phenotypic plasticity exhibited by plants. Such malleability, the ability to change and adapt in response to variations in the underground environment, means that many root traits are tailored by their environment.

With increasing evidence that environmental heterogeneity is increasing, due to climate change effects, it is important to investigate how roots will respond in different environments. In particular, root traits linked to shoot growth and dry matter production should be investigated in order to understand how the roots' plasticity can have a role in enhancing grain yield in a dynamic soil environment and whether roots' morphological and physiological plasticity is linked to a shoot response and to consequent dry matter production. This is an important and increasingly relevant subject of research especially in paddy cultivation where there is an increasing demand to grow rice with reduced water application.

With regard to dry matter production in rice, there are several reports that show that many shoot morphological and physiological traits contribute to high yield, such as larger sink size, higher leaf area index, larger leaf area duration, higher photosynthetic rate, slower leaf senescence, stronger lodging resistance, greater biomass accumulation before heading, and more translocation of carbohydrates from the vegetative parts to the panicle during the grain-filling period. Fewer studies have been conducted on root morphological and physiological traits that may be linked with shoot growth and yield. Studies so far conducted mainly consider the effects of genetic variability on root morphological and physiological traits [6].

These studies do not reflect the effects of the soil environment that could greatly alter root architecture since root systems' growth and functioning are regulated not only by genetic programs but also are influenced by abiotic and biotic stimuli [7]. In particular, root traits that are linked to shoot growth and dry matter production should be investigated in order to understand the roots' plasticity and their possible role in enhancing grain yield in a dynamic soil environment.

Given the climate variability, methane emission from paddy fields, and water constraints facing the rice sector in many countries, the most important crop management practice which has got major attention, both from farmers and researchers, is the cessation of continuous flooding, either through intermittent irrigation or by keeping soil moist but not continuously inundated. The intermittent irrigation of rice is not something new, and recently it has been supported in some rice-producing countries in an attempt to reduce the volume of irrigation water used [8].

Some earlier reports on the effects of cessation of flooding have suggested that under unsaturated soil moisture conditions, there is a significant decrease in dry matter production and grain yield for rice [9, 10]. It is suggested that this could be due to a rapid rate of loss of nitrogen facilitated by nitrification and denitrification [11]. However, others have reported a higher yield correlated with intermittent irrigation during the vegetative stage when accompanied by SRI management practices (transplanting younger seedlings 1–2/hill, avoiding continuous soil saturation, aerating soil, and applying organic manure as much as possible) due to healthy root growth and greater soil microbial activity [12, 13] and even under post-anthesis water-deficit conditions when organic matter has been applied to the soil [14]. It

has been reported that skillful soil drying post-anthesis improves remobilization of carbon reserve and grain filling [15].

Such inconsistent reports on the effects of intermittent irrigation and/or nonflooded water regimes for rice production leave some important questions unanswered since they did not assess how rice plants' roots and shoots will respond, respectively and jointly, when subjected to different soil moisture conditions in combination with varying soil microbial condition. There is limited information whether these responses, if they occur, will lead to greater dry matter production or to less and whether these recommended practices and resultant morphological and physiological plasticity can have any contribution toward mitigation of methane emission from the rice fields. This is a research area warranting investigation.

This chapter reports some initial research findings on the plastic response of rice plants that resulted due to change in water regimes and microbial density. Further, it illustrates the causal relationship between rice root and shoot growth and also discusses the implication of root plasticity for mitigation of methane emission from rice fields. The study was conducted to assess the effects of differences in the soil biota in conjunction with alternative water management practices in rice.

In this context, the term alternative water management practices have been introduced here as "water-saving irrigation" to describe producing more rice with less water. This involves (i) reducing the depth of ponded water; (ii) keeping the soil just saturated, not continuously flooded; or (iii) employing intermittent irrigation or alternate wetting and drying, i.e., allowing the soil to dry out to a certain extent before reapplying irrigation water.

2. Methodology

Black clay soil was collected from the rice research farm of the Asian Institute of Technology where the previous crop grown was rice. The average composition of the soil was 10.2% sand, 23.2% silt, and 66.2% clay, with pH (1.1) of 5.0. Organic C was 1.38%, total N 0.14%, available P 11 mg kg^{-1}, and available K 212 mg kg^{-1}. Cation exchange capacity was 22.6 cmol kg^{-1}.

After air drying, the soil samples were crushed, and crop residues were removed by hand. In each plastic pot (60 cm high with diameters 50 cm at the top and 40 cm at the bottom), 65 kg of soil was placed. All pots were flooded by the addition of distilled water to a depth of 3–4 cm for a week before transplanting and were dressed with 138 mg *N* and 12.3 mg *P* per kg of soil applied in NPK fertilizer 16:16:0 as basal application and urea (46:0:0) at 15 and 45 days after transplanting (DAT). Single 15-day-old seedlings (variety *Pathumthani*: maturity period = 120 days, nonphotosensitive) with two fully expanded leaves grown in a dry seedbed were transplanted within 2 hours of uprooting from the nursery seedbed with a sowing depth of 1.5 cm. Water treatment was started 7 days after transplanting when transplanting shock had disappeared.

3. Experiment 1

The first experiment was set up to evaluate the effect of water regimes. Root length density, root-oxidizing activity rate, and chlorophyll content of lower leaf were studied under four water regimes:

1. Intermittent flooding (IF-I)—Pots were maintained with 5 cm depth of water from the soil surface and maintained for 12 days, then drained for 3 days, and

again reflooded with the same depth of ponded water. Three 3-day drying periods were provided at 19, 34, and 50 days after transplanting (DAT) followed by flooded water treatment (5 cm water depth continuously) until maturity.

2. Intermittent flooding (IF-II)—In another pot, similar procedure like IF-I was followed for 5 times at 19, 34, 50, 66, and 82 DAT, followed by flooded water until maturity.

3. Nonflooded (NF)—Pots were maintained under the continuous nonflooded condition and at field capacity (FCp) at the rooting zone.

4. Continuous flooded (CF)—5 cm depth of ponded water was maintained until maturity.

For root study, soil samples were collected from pots at flowering (72 DAT) and at 20 days after flowering (DAF), i.e., at 92 DAT, from the upper (15–20 cm) and subsoil (35–40 cm) layers for root length and root-oxidizing activity.

Roots after being washed with water were cut into small pieces. The root length was calculated using the line intersection method described by Tennant [16]. Root length density (RLD) was then calculated by using the formula: RLD = RL/V, where RL = root length and V = volume of the soil core soil.

Root activity (ROA) rate was measured by assaying the oxidation of alpha-naphthylamine. Five grams of fresh roots were transferred into a 150 ml flask containing 100 ml of 20 mg l^{-1} alpha-naphthylamine. The flask was incubated for 4 hours at room temperature (25 ± 1°C) in an end-over-end shaker. After incubation, the aliquots were filtered, and 2 ml of aliquots was reacted with 10 ml of 0.1% sulfanilic acid and then with 2 ml of 50 ppm $NaNO_3$. The resultant color was measured by spectrophotometer at 530 nm, and the value is expressed as μg (g Fw)$^{-1}$ h^{-1}.

Chlorophyll content of the flag leaf and of the third leaf was recorded at intervals of 7 days from flowering to physiological maturity stages, using a chlorophyll meter (SPAD 502; Minolta Corp; Tokyo) calibrated by using spectrophotometric assays in order to determine the exponential equation to directly convert its output to leaf chlorophyll concentration [16]. These data were collected from undisturbed pots for each treatment combination which had not been used for root study and nitrogen estimation.

4. Experiment 2

In another experiment, IF-I, IF-II, and CF water regimes were tested with three soil conditions that differed in soil microbial density. The three soil conditions were untreated normal soil (NS), autoclaved soil (AUS) in which soil biota had been mostly minimized, and soil in which the abundance of soil biota had been enhanced by applying a solution of effective microorganisms (EMS).

A commercial preparation of effective microorganisms known as "Bio EM" was obtained from EMRO Thailand. The Bio EM was prepared by using a concentrated stock solution of effective microorganisms, EM-1. The formulation of EM-1 is kept secret, although according to one of the EMRO centers (BIONOVA Hygiene GmbH, Stans, Switzerland), EM-1 contains 1.3×10^7 colony-forming units (cfu) of lactic acid bacteria ml^{-1}, 3.3×10^4 cfu photosynthetic bacteria ml^{-1}, and 1.3×10^4 cfu of yeast ml^{-1}. Bio EM was processed from EM-1 by fermentation under anaerobic conditions with water and sugarcane molasses for 7 days.

In the EMS soil pots, the Bio EM solution was first applied at 7 DAT, with 6.75 ml of concentrated EM solution mixed in 4.5 l of water. Before the start of any irrigation of these trials with EM-treated soil (EMS), 0.5 l of this mixed solution was applied. After that, water levels were maintained in all EMS pots according to the treatment schedules. The EM application was repeated at weekly intervals until 1 month before harvesting, unless a draining period coincided with the EM application. EM application was avoided during draining periods and was applied with the next scheduled irrigation, immediately following a drainage period.

For further experimental details, see [17].

5. Results

5.1 Effects of varying water regimes

The result indicated significant effects of varying water regimes on root length density, both at the upper and subsoil layer. At flowering, there was no difference recorded in the root distribution in the upper soil depth in the intermittent irrigation followed until vegetative stage (IF-I) and continuously flooded treatments (CF), and in these treatments, most of the roots were observed to be distributed in the upper soil layer. In contrast, fewer roots were observed at lower soil depth in the CF than the IF-II. The distribution pattern was different in the nonflooded treatment (NF) treatments compared to the other three water regimes. In this treatment, almost half of the total root length density was distributed at the lower soil depth. At the later growth stage, a drastic reduction in root growth was observed under the continuously flooded treatment compared to other water regimes at both soil depths. Almost 70% root reduction was observed under the continuously flooded condition in the upper soil depth (**Figure 1**).

Further, it was observed that the physiological activity of the roots, i.e., root-oxidizing activity rate, was higher in the IF-I water regime than in the continuously flooded condition and continuously intermittent irrigation at a later growth stage (**Figure 2**). The experiment revealed that there was a positive correlation between chlorophyll content of lower leaves and root activity in all water regimes (**Figure 3**) depicting the causal relationship with those shoot traits which are linked to increased dry matter production.

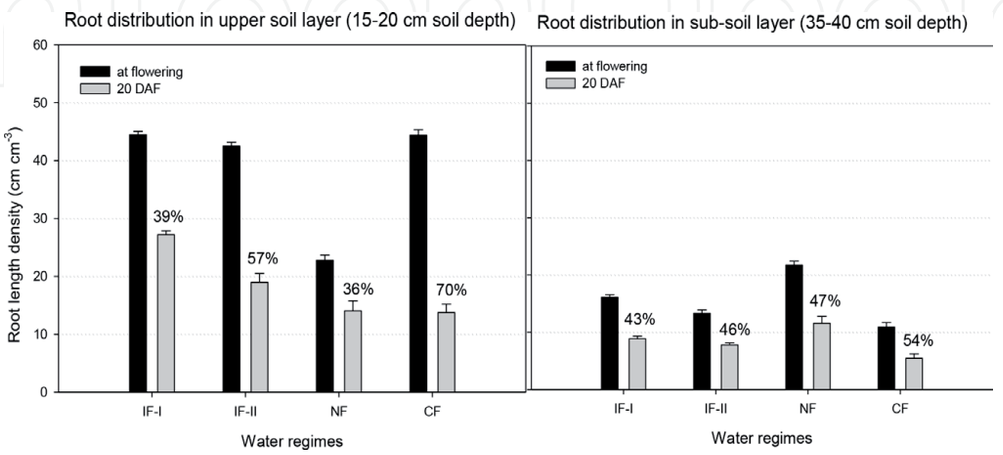

Figure 1.
Root length density (RLD) (cm/cm³) in the upper and subsoil layer at flowering and 20 days after flowering of rice plant grown in pots under different water regimes (IF-I, IF-II, NF, and CF). The number above the gray bars shows percentage reduction in root length density at 20 days after flowering. Error bars show SE.

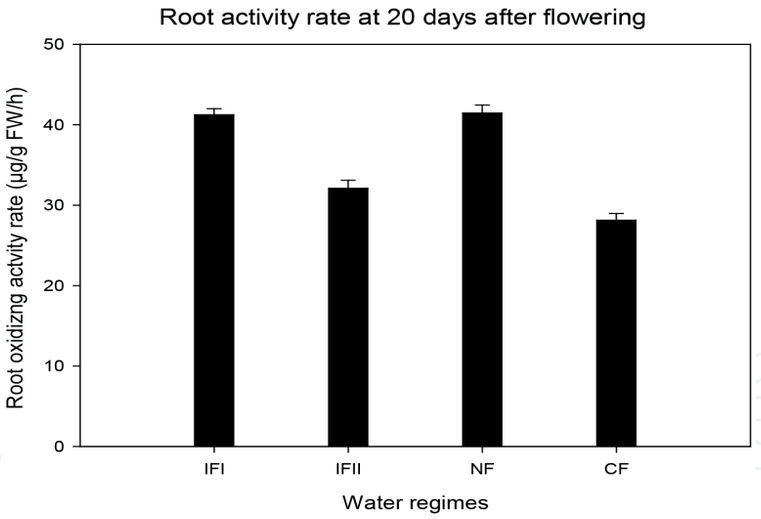

Figure 2.
Root-oxidizing activity rate under varying water regime. IF-I, intermittent draining three times; IF-II, intermittent draining five times; NF, nonflooded; and CF, continuous flooding.

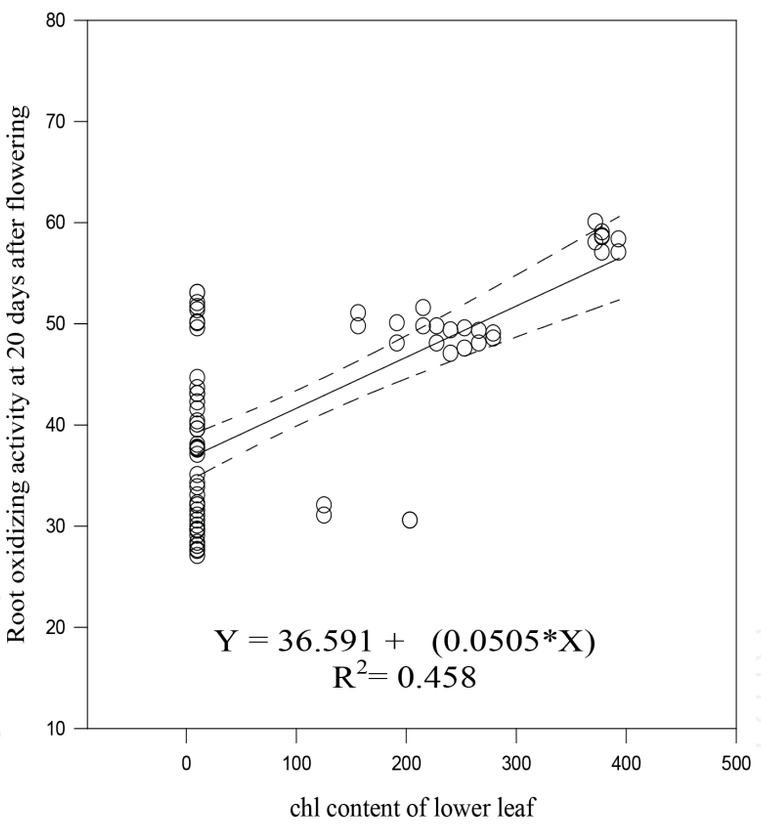

Figure 3.
Relationship between chlorophyll content of lower leaf and root-oxidizing activity at 20 days after flowering.

5.2 Effects of varying water regimes and soil microbial density

EMS treatment increased the number of spikelets/panicle and filled grains/panicle under all water regimes. Also, at the flowering stage, both root length density and root activity were higher in EM-treated rice plants under all three water regimes evaluated. However, at later growth stages, the EM-treated plants grown under IF-I and IF-II showed lower root activity rates compared to plants that were grown in autoclaved or normal soil (**Table 1**).

Water regimes	Soil conditions		
	Normal soil	**EM-treated soil**	**Autoclaved soil**
Number of spikelets per panicle			
IF-I	227.75 ± 2.09	244.00 ± 1.90	203.63 ± 1.82
IF-II	187.38 ± 1.16	196.13 ± 1.72	166.50 ± 1.22
NF	191.50 ± 1.27	206.25 ± 1.74	173.88 ± 2.36
Filled grains per panicle			
IF-I	227.75 ± 2.09	244.00 ± 1.90	203.63 ± 1.82
IF-II	187.38 ± 1.16	196.13 ± 1.72	166.50 ± 1.22
NF	191.50 ± 1.27	206.25 ± 1.74	173.88 ± 2.36
RLD at 15–20 cm soil depth (at flowering)			
IF-I	45.46 ± 0.78	63.51 ± 1.75	54.83 ± 1.36
IF-II	45.53 ± 1.59	62.06 ± 1.26	53.38 ± 1.21
NF	22.77 ± 1.61	23.57 ± 1.70	22.18 ± 2.03
Root-oxidizing activity rate (μg/g FW/h)at flowering			
IF-I	63.40 ± 0.74	66.31 ± 0.77	64.35 ± 0.93
IF-II	63.10 ± 0.35	66.53 ± 0.38	64.20 ± 0.40
NF	53.50 ± 0.49	59.23 ± 0.43	52.31 ± 0.56
Root-oxidizing activity rate (μg/g FW/h)at 20 days after flowering			
IF-I	42.28 ± 0.57	40.01 ± 1.49	58.30 ± 0.35
IF-II	33.1 ± 0.33	32.10 ± 0.58	33.54 ± 0.46
NF	41.31 ± 0.57	40.15 ± 0.60	49.70 ± 0.44
Grain weight per plant (gm/pot)			
IF-I	165.74 ± 4.07	186.23 ± 5.2	198.27 ± 4.37
IF-II	101.75 ± 7.28	115.41 ± 7.11	103.37 ± 6.11
NF	116.46 ± 2.19	134.59 ± 5.6	125.71 ± 1.58
Total biomass (g/plant)			
IF-I	341.71 ± 10.22	363.67 ± 15.57	398.9 ± 20.76
IF-II	215.73 ± 7.67	201.38 ± 9.37	218.61 ± 4.59
NF	248.14 ± 9.75	257.62 ± 5.29	243.95 ± 11.13

IF-I, intermittent draining three times; IF-II, intermittent draining five times; and NF, nonflooded, and varying soil conditions: NS, normal soil; EMS, soil treated with effective microorganisms solution; and AUS, autoclaved soil on morphological and physiological root, shoot traits, and grain yield. Values show mean ± SE.

Table 1.
Effect of varying water regimes and soil types on morphological and physiological root, shoot traits and grain yield.

To gain further understating, soil nitrogen status was studied. At flowering, an appreciable increase in the concentration of available nitrogen (*N*), and of NH_4^+ in particular, was found in the rhizosphere soil with EMS treatment under IF-I and IF-II water regimes, but not with NF (**Table 2**). This indicates the possible impact of drying and rewetting of soil on the microbial populations. It seems that repeated application of EM solution in the EMS pots increased the amount of soil-available *N* due to the rapid rate of mineralization. However, at 20 days after flowering, the concentration of *N* was higher in the AUS treatment compared to EMS and NS

	Intermittent draining, three times (IF-I)		Intermittent draining, 5 times (IF-II)		Nonflooded (NF)	
	F	20 DAF	F	20 DAF	F	20 DAF
Autoclaved soil (AUS)	48.76 (64.62)	55.3	37.09 (47.19)	13.72	76.77 (39.71)	48.48
EM-treated soil (EMS)	37.21 (91.09)	23.38	25.23 (64.87)	8.1	66.64 (42.6)	24.24
Normal soil (NS)	56.32 (56.31)	43.62	41.1 (42.6)	10.66	74.71 (37.33)	36.04

IF-I, intermittent draining three times; IF-II, intermittent draining five times; and NF, nonflooded, and soil types: NS, normal soil; EMS, soil treated with effective microorganisms solution (EM); and AUS, autoclaved soil on soil nitrogen status (NH_4^+ and NO_3^-) – N (mg kg^{-1}) at flowering (F) and total available nitrogen (mg kg^{-1}) at 20 days after flowering (DAF). The number under parenthesis shows the content of NH_4^+ at flowering.

Table 2.
Effect of varying water regimes and soil types on soil nitrogen status.

under IF-I and NF water regimes. Significant differences at both growth stages were observed in the IF-I and NF water regimes, but not in the IF-II regime, probably due to the higher rate of nitrogen loss from the soil, facilitated by a greater number of repeated drying-wetting cycles.

Within IF-I, the low availability of *N* in the EMS soil at 20 days after flowering indicated that either (a) the plants' *N* uptake rate was higher in EMS soil compared to AUS and NS soil, or (b) competition between plant roots and soil microbes was increased for the *N* at later growth stages due to higher microbial population and thus to a higher rate of immobilization of NH_4^+, or (c) the rate of denitrification was increased after reflooding due to reduced soil conditions and a relatively higher rate of oxygen demand by microorganisms. Upon flooding, under the reduced soil conditions of IF-I, the possibility of leaching loss of NO_3^- was very small. Hence, it seems that either this *N* was taken up by the plant or any remaining nitrate moving downward after reflooding could have been intercepted by anaerobic microorganisms to use as terminal electron acceptors for anaerobic respiration.

In the IF-II water regime, soil nitrogen content was lower than either IF-I or NF water regimes, probably due to an increased rate of nitrogen loss caused by the greater number of times that draining-reflooding was done, facilitating a higher rate of denitrification and immobilization compared to the IF-I and NF water regimes.

Assessment of the available forms of *N* in AUS and NS soils under IF-I and IF-II water regimes at flowering stage indicated that almost half of the nitrogen was present in NO_3^- form, whereas with EMS, the percentage of NH_4^+ was greater (**Table 2**). The higher percentage of NH_4^+ in the EMS treatments reflects a higher rate of mineralization due to higher soil microbial populations.

The presence of significant amounts of NO_3^- in the autoclaved and normal soil in IF-I treatments at flowering indicates that in soil planted with rice, the O_2 released from the rice roots may also be supporting nitrification along with that produced in the upper oxygenated soil layer. Transpiration of the rice plants causes mass flow of water, resulting in mass flow of NH_4^+ as well toward the roots, supporting nitrification even under the anaerobic soil layer. As indicated earlier, a combination of NH_4^+ and NO_3^- leads to higher yields, greater by 40–70%, than does provide the same amount of N only as NH_4^+ [18]. Therefore, it appears that higher root activity for a longer duration, especially at the grain-filling stage, may help

plants to get more of both forms of nitrogen even under flooded conditions, by supporting higher nitrification through the better supply of oxygen to the rhizosphere. This could be another reason for getting higher grain yield under the IF-I water regime than the IF-II and NF water regimes.

The study further revealed that the kinetics of available *N* and NH_4^+ was somewhat different in nonflooded soil (NF). The total available *N* was similar to that of IF-I, but it was present mainly in the form of NO_3^-. At the flowering stage, there was no effect of soil treatments on the available *N* content in the NF treatment. However, at 20 DAF, the EMS treatment had less *N* than AUS and NS treatments. Some case studies have demonstrated that the nitrogen requirement of microorganisms that decompose organic matter in aerated soils is higher than for decomposers in flooded soils, which results in higher net N immobilization in aerobic soils than in flooded soils [19]. This might be the reason for low soil N status in the EMS treatments compared to AUS and NS and so the lower root activity and early senescence. However, the biomass production was similar in all soil types under the NF water regimes (see **Table 1**), and the highest grain weight was recorded in the EMS and AUS treatments who received IF-I treatment.

Further, it can be seen that although there was no limitation of soil nitrogen in the NF water regimes, still plant biomass was not as significant as seen with IF-II. The possible reason could be a slower growth rate during the vegetative stage and lower cytokinin content in the roots. It is known that cytokinin content is regulated by soil nitrogen content and that the production of cytokinin as well as biomass is stimulated by having mixed source of nitrogen rather than only single source.

6. Discussions

6.1 Morphological and physiological plasticity of root architecture

Root length density—an important parameter of root morphology reflecting root architecture—is known to influence not only root-microbial interaction but also the physiological activity of roots, which plays an important role in increasing plants' photosynthetic capacity [20, 21]. Researchers have demonstrated that rice plants with higher root-oxidizing activity rate during their later growth stages have higher grain yield [22]. However, these findings were derived from rice plants with hybrid and "super" rice varieties which are known to have greater root activity than any traditional varieties [23].

Our preliminary studies [17] showed the significant effects of management practices such as intermittent irrigation or nonflooded water regimes on root development. The root architecture—defined here as root length density—significantly changed with mild water deficit. The response was not just at morphological level, but root activity also changed due to the effect of water and soil-available nitrogen and consequently also affected yield contributing parameters and finally grain yield. The root activity was higher in those plants who had higher chlorophyll content in their lower leaves at the later growth stage. Indeed this was related to high soil nitrogen content at later growth stage.

Many reports suggest that exploitation of soil resources through root activity may consume more than half of the available photosynthate in mature plants [24]. Given competing demands for internal plant resources for photosynthesis, support, defense, and reproduction, it is reasonable to expect that plastic response has favored plants that directed root activity to exploit efficiently, i.e., with a favorable balance of resource investment versus resource acquisition.

Knowing the effect of soil microbial density on soil nitrogen status, on important root traits under alternative soil water regimes, and the resulting effects on plant growth and performance helped to clarify the adaptive physiological response of plants under such different conditions.

It appeared that the combination of higher root-oxidizing activity rate, higher availability of NH_4^+/NO_3^- nitrogen, and higher chlorophyll content of the lower leaves at the later growth stage was one of the reasons for having higher yield under the two water conditions, IF-II and NF, compared to IF-II.

But we also noted that plants grown in autoclaved soil, either with IF-I or NS, had higher root activity rates than the other soil treatments. This increment did result in higher grain yield than with the other soil conditions; however, even with EM application, the root activity rate at a later growth stage was reduced significantly, but grain yield was similar to that of AUS soil treatments.

It seems that this physiological response of roots, i.e., their root activity rate, depends on the relative costs and benefits to the plant. If the supply of photosynthate to the roots, which comes mostly from the lower leaves of the plant, is restricted, or if the soil is limited in its nutrient availability and roots are unable to supply sufficient nutrients to the aboveground parts, the plasticity of response of plants' roots—either morphological proliferation or higher physiological activity—will be a burden for the plant.

Ultimately, the cost to the plant will depend on what is actually limiting its growth, whether nutrients or photosynthate supply. Therefore, the physiological basis of the plasticity of root and shoot growth needs to be understood inclusively within the context of environmental variables they are encountering with.

These works were the preliminary investigation and warrant further investigation at field level under different soil and weather conditions. However, the initial findings clearly showed that root architecture and root activity is greatly influenced by soil environment, particularly by water and soil microbial conditions. This flexibility arises due to the modular structure of roots which enables root deployment in zones rich in water and nutrients. The genetic control on this root deployment is still largely unknown, although the gene ANR1 is involved in the first stages of the nitrate (NO_3^-) signaling system when NO_3c- levels are locally enhanced [25]. This needs to be further studied under the subject of epigenetics.

6.2 Root plasticity under intermittent irrigation and opportunities for mitigation of methane production in the rice field

While there is a need to continue research to identify and/or induce more productive genotypes in general, concern for dealing with climate change should prompt more research particularly on how best to modify crop management to take advantage of plants' inherent plasticity of morphological and physiological response to environmental influences that would otherwise be limiting factors and constraints.

It is known that up to 90% of the CH_4 emitted in rice paddies is released through rice transport [26], while between 19 and 90% of the CH_4 produced is oxidized, with up to 75% of the CH_4 oxidation taking place in the rhizosphere [27]. Accordingly, strategies to lower net CH_4 emission from rice fields include reduction of CH_4 production, increasing CH_4 oxidation, and lowering CH_4 transport through the plant. Among the CH_4 emission mitigation strategies that do not compromise rice productivity, the introduction of drainage periods during the crop cycle appears to be the most efficient [28]. Thus, it has been estimated that intermittent drainage periods by applying intermittent irrigation in poorly drained rice fields could reduce 10% the agricultural CH_4 emissions [29].

It is expected that the higher root activity rate for a longer duration, as appeared in our studies, should further enhance CH_4 oxidation in the rhizosphere because of the prolonged oxygenated rhizosphere. This benefit will be relatively higher under intermittent irrigation water regimes, but even under flooded condition, a relative mitigation benefit can be achieved through minimizing intra-hill competition since minimizing intra-hill competition can also enhance root activity [30].

In the present study, aerobic soil was maintained for some period in IF-I, IF-II, and for the whole crop growth period in the NF water regime. It could be assumed that under continuously flooded water regimes, the soil would be anaerobic except 2–5 cm depth from the surface of the soil. But even under this condition, the root length density was better at 15–20 cm soil depth at the flowering stage (**Figure 1**). It shows that oxygen concentration required for the development of laterals was present in this zone even under continuously flooded water regimes.

The earlier findings suggest that for an aerobic rhizosphere, spacing is critical along with the number of primary roots per plant [31]. For example, if the number of primary roots is 500, and the hill spacing is 25 × 25 cm, then the numbers of root/cm^2 = 0.8 root cm^{-2}. Thus for FO_2 A_R (where FO_2 = flux of oxygen across root surface, and A_R = surface area of roots capable of absorption) = 0.2 nmol s^{-1} (which is standard rate under flooded condition), the rate of release of oxygen will be 160 pmol cm^{-2} (soil surface) s^{-1}. This amount of oxygen is sufficient for the growth of laterals as well as nitrogen uptake by the plants in the form of ammonium and nitrate under flooded condition.

Typically, the maximum rate of nitrogen uptake by rice crop are ≤5 kg h^{-1} day^{-1} [32] or 40 pmol cm^{-2} (soil surface) s^{-1}. Therefore, if half the oxygen released from the roots was used to nitrify ammonium in the rhizosphere ($NH_4^+ + 2O_2 \rightarrow NO_3^- + 2H^+ + H_2O$), and half the nitrate produced was recovered by the roots, an oxygen release of 160 pmol cm^{-2} (soil surface) s^{-1} would be sufficient to nitrify half the nitrogen by the roots and also methane oxidation. This would facilitate uptake of nitrogen in the form of nitrate and ammonium as well for higher biomass production along with methane emission reduction from paddy fields. Therefore, aerobic rhizosphere can be maintained even under shallow flooded condition by minimizing intra-hill competition, by transplanting fewer seedlings/hill with wider spacing.

In addition, intermittent irrigation or keeping soil "preferably moist" or in nonflooded condition will reduce aerenchyma formation rate. Since the aerenchyma acts as a channel for oxygen transport from the atmosphere to the roots and CH_4 transport from the site of production to the atmosphere, therefore, reduced aerenchyma formation will lead to lowering CH_4 transport through the plant.

These benefits become more relevant in the prospective scenario where rice production needs to be increased with both reduced water applications and reduced "climate-forcing" practices.

These initial findings are opening up many possibilities for better understanding of plants' growth response and root plasticity under varied soil environments which could be exploited and manipulated to enhance crop production through enhanced root/rhizosphere activity.

Since, agronomic crop management practices (avoiding continuous soil saturation, minimizing intra-hill competition, applying effective microorganism, organic manure, aerating the soil, etc.) are seen to increase root growth and yield from practically any variety. Our research suggests that positive responses can be induced through appropriate water management practices and with an increased microbial density that can increase the total root and shoot growth and plant biomass. It also suggests that the roots and shoots are not necessarily in a zero-sum relationship, as posited by harvest index thinking; with appropriate agronomy, there can be positive

feedbacks between each, as evident from this study. Therefore, such management practices should be explored in detail to gain a better understanding of root and rhizosphere activity.

7. Conclusions

Climate change is altering the growing environments for plants, particularly aboveground, but there are also belowground effects as changes in precipitation and in ambient temperature have a strong influence on soil conditions. Plant species are genetically programmed to adjust to the novel conditions through phenotypic plasticity. While there is a need to continue research to identify and/or induce more productive genotypes in general, concern for dealing with climate change should prompt more research particularly on how best to modify crop management to take advantage of plants' inherent plasticity of morphological and physiological response to environmental influences that would otherwise be limiting factors and constraints.

Our results and discussion document that rice root morphology and physiology and consequently rice shoot growth are significantly affected by variations in soil water conditions. Root architecture and roots' oxidizing activity rate are important factors--influencing higher yield--are quite plastic in nature and vary considerably with varying water regimes and with varying soil microbial population. Modifying water management to take advantage of plants' inherent plasticity of morphological and physiological response can be one of the adaptive strategies for achieving higher yield under reduced water condition along with mitigation of methane production from rice fields. Such an investigation would be useful to develop alternative crop management practices that will reduce "climate forcing" and will provide better ecosystem services.

Conflict of interest

The authors declare no conflict of interest.

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